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FULL PAPER

Lyophyllum shimeji, a species associated with lichen pine forest in northern Fennoscandia

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Abstract Phylogenetic relationships of *Lyophyllum* section *Difformia* were inferred using internal transcribed spacer (ITS) and large sub-unit (LSU) sequence data of specimens from Fennoscandia and Japan. Sequence analyses show that the delicacy mushroom *Lyophyllum shimeji*, hitherto only known from East Asia, occurs in Fennoscandia and that it is confined to Scots pine forests on lichen-clad sandy soil. Also, *Lyophyllum decastes* and *L. fumosum*, two species described from Europe, have a wide distribution and are represented in Japan. Within both these species sequence variation indicates that more taxa should be recognized. The observed phylogenetic differences correlate strongly with habitat, conifer or deciduous forest, but also to some extent with geographic origin. The identity of the species *Lyophyllum loricatum* remains unclear and further sequences from specimens fitting the original description are needed to resolve its taxonomic status. The phylogenetic results suggest that ecology is an important character when discriminating between species in *Lyophyllum* section *Difformia*.

Keywords Delicacy mushroom · Hon-shimeji · *Lyophyllum decastes* species complex · Taxonomy

Introduction

Lyophyllum decastes (Fr.) Singer is generally regarded as a species complex with many names included and also a great deal of taxonomic confusion (e. g. Singer 1986). One of the species belonging to this complex is *L. shimeji* (Kawam.) Hongo with known distribution in the Far East. In Japan the common name for this species is hon-shimeji (meaning real shimeji) and the mushroom has been recognized as a delicacy for centuries. Since the mid-twentieth century a decline in the fructification of *L. shimeji* has been observed (Fujita et al. 1982; Kawai 1997; Yamanaka 2009). Several causes for this decline have been suggested, such as the loss of suitable forests due to infections by the pine wood nematode (*Bursaphelenchus xylophilus*) or changes in forest management (Ohta 1994; Kawai 1997; Kosaka et al. 2001; Yamanaka 2009). Today wild-grown hon-shimeji is available only through a few dealers specializing in delicacy mushrooms and is almost only served in high-class restaurants (Ueda, personal communication). Great efforts have been made to master the cultivation of hon-shimeji, and the past decade has seen some progress (Ohta 1994; Yamanaka 2009), although yields have been relatively low.

The species in the *L. decastes* complex are very similar in both macro- and micro-morphology. In addition there is also a large amount of intra-specific plasticity in terms of basidiocarp size and form, gill attachment to the stem, and in coloration. This is probably a major reason why the species are often mixed up both in the literature and in herbaria around the world (Moncalvo et al. 1990; Kalamees 2004; Yamanaka 2009).

Lyophyllum section *Difformia* and the *L. decastes* complex have been the subject of many studies using different techniques such as comparative morphology, numerical analysis based on electrophoretic patterns of isozymes, culture studies, and large sub-unit (LSU) sequence data (Clémençon and Moncalvo 1990; Moncalvo and Clémençon 1992, 1994; Moncalvo et al. 1990, 1993).

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Five morphologically distinct taxa in the *L. decastes* complex in Europe and Japan were recognized by Moncalvo and Clémençon (1992) and named T1–T5. Later (Moncalvo and Clémençon 1994) the five taxa were confirmed using numerical analysis by combining isozyme and culture data, but no taxonomic revision was proposed. *Lyophyllum shimeji* was found by Clémençon and Moncalvo (1990) to produce two types of mycelia with widely different culture characteristics, indicating the occurrence of two species. Using mating tests and data from mitochondrial rDNA sequences Maeta et al. (2008) showed that *L. shimeji* probably consists of two biological species. The section *Difformia* is here used according to Moncalvo and Clémençon (1994), thus limiting the section to the species in the *L. decastes* complex; viz. *L. decastes*, *L. fumosum* (Pers.) P.D. Orton, *L. loricatum* (Fr.) Kühner, and *L. shimeji*.

Fries (1818) described *L. decastes* as a species growing in heathland next to the roots of an oak, "In ericetosis ad radices Quercuum". In Japanese, its common name "hatake shimeji" means, approximately, field shimeji and that it grows in arable land (Yamada, personal communication), which is also the habitat most commonly referred to in the literature. In the Nordic countries it is most often regarded as a common species and is found in both deciduous and coniferous forests, along roadsides, and in parks and grassland, but also in heathland (Ryman and Holmåsen 1994; Vesterholt and Ludvig 2008).

Lyophyllum fumosum was introduced by Persoon (1801) and described as a species occurring here and there in the forest, growing in grass "passim in sylvis, locis graminosis". The name was accepted by Fries (1821) and he gave the habitat as pine forest, birch forest, and similar places, in rough terrain, "In pinetis, betuletis similibusque, locis asperis". In Japan the common name is "shaka-shimeji", meaning Buddha shimeji, and it grows in mixed forest with *Pinus* (Imazeki et al. 1988). In the Nordic countries it is usually referred to as a species found in coniferous forests and it is considered as occasional or rare (Hallingbäck and Aronsson 1998; Nylén 2001). However, Ingelström (1940) calls it a beech forest species, and Vesterholt and Ludvig (2008) report it from both deciduous and coniferous forests and also from parks.

Fries (1838) described *L. loricatum* as a rare species growing in shady hazel groves in rocky places, "In coryletis umbrosis, montosis raro". In Japan the common name is "kuro-shimeji", blackish shimeji, and it seems to be a rare species possibly confined to Hokkaido (Yamada, personal communication). In the Nordic countries it is said to grow in deciduous forests and also on burnt ground (Hallingbäck and Aronsson 1998). In Vesterholt and Ludvig (2008) it is treated as a variety of *L. decastes*.

Lyophyllum shimeji grows in mixed *Pinus densiflora–Quercus serrata* forests in Japan. It is also widely distributed in China and Korea (Fujita et al. 1982; Yamanaka 2009). So far the species has not been reported outside that area.

The species in *Lyophyllum* have traditionally been regarded as saprotrophic (Singer 1986, Vesterholt and Ludvig 2008). Today several of the species in the *L. decastes* complex are considered as ectomycorrhiza formers. Trappe reported as early as 1962 that *L. immundum* formed ectomycorrhiza with *Pinus sylvestris*. *Lyophyllum shimeji* has been described to form facultative mycorrhiza (Ohta 1994) and *L. decastes* has been described to form ectomycorrhiza in vitro with *Pinus pinaster* (Pera and Alvarez 1995). Also *L. fumosum* is considered as putatively ectomycorrhizal in Japan (Yamada et al. 2001).

In 2008 the Japanese mycologist Etsuko Harada visited pine forests in northern Sweden and encountered a fungus that to her looked very much like hon-shimeji, *Lyophyllum shimeji*. During 2009 further collecting was undertaken in both Japan and Fennoscandia. The present study reports the results from a molecular phylogenetic study of specimens belonging to the *Lyophyllum decastes* complex, with the specific aim of confirming whether *L. shimeji* occurs in Fennoscandia and revealing its phylogenetic relationships with other Nordic species in section *Difformia*.

Materials and methods

Taxon sampling

The specimens used for phylogenetic analyses were obtained through collecting in Sweden and Japan. In addition, specimens from herbariums GB, L, and O (Holmgren et al. 1990), and two commercially sold cultivars from Japan were sequenced. Field collections are deposited in Herbarium GB, Department of Plant and Environmental Sciences, University of Gothenburg.

Sequences of 30 specimens from section *Difformia* and one specimen of *L. semitale* (Fr.) Kühner were generated. The specimens were selected to represent *Lyophyllum decastes* and *L. fumosum* from both deciduous and coniferous forests. Two specimens identified as *L. loricatum* were included. Data on the sequenced specimens are provided in Table 1.

Sequences of the internal transcribed spacer (ITS) and LSU regions of nine specimens or culture strains of *L. shimeji*, *L. decastes*, and *L. fumosum* were downloaded from GenBank and the Japanese database NITE Biological Research Center (NBRC). Six sequences from earlier molecular phylogenetic studies of *Lyophyllum* and *Agaricales* (Hofstetter et al. 2002; Moncalvo et al. 2002; Matheny et al. 2006), representing *Lyophyllum ambustum* (Fr.) Singer, *L. anthracophilum* (Lasch) M. Lange &

Table 1 Data of specimens sequenced in this study

Species	Collection ID./origin/herbarium	Ecology, substrate	GenBank no.
Lyophyllum shimeji	Cultivar/Jpn	Unknown	HM572522
L. shimeji	Sundberg 20091007/Jpn/GB	*Pinus*/*Quercus* forest	HM572528
L. shimeji	Fällman 2009-09-27/Swe/GB	Lichen *Pinus* forest	HM572536
L. shimeji	LAS 00-062/Swe/GB	Lichen *Pinus* forest	HM572523
L. shimeji	Lipovac 20090911/Swe/GB	Lichen *Pinus* forest	HM572534
L. shimeji	Eilertsen 20090908/Swe/GB	Lichen *Pinus* forest	HM572531
L. shimeji	Sundberg 20090813a/Swe/GB	Lichen *Pinus* forest	HM572524
L. shimeji	Sundberg 20090813b/Swe/GB	Lichen *Pinus* forest	HM572532
L. shimeji	Sundberg 20090813c/Swe/GB	Lichen *Pinus* forest	HM572535
L. shimeji	Anttila 20090921/Fin/GB	Lichen *Pinus* forest	HM572526
L. shimeji	Karlsson 20090915/Swe/GB	Lichen *Pinus* forest	HM572527
L. shimeji	Olausson 20090922/Swe/GB	Lichen *Pinus* forest	HM572533
L. shimeji	Domeij 20090913/Swe/GB	Lichen *Pinus* forest	HM572525
L. shimeji	Haukebø 1982/Nor/O	Coniferous forest	HM572529
L. shimeji	Olsen 19821006/Nor/O	On path in forest	HM572530
L. decastes	Brunsson 19920924/Swe/L	Grass lawn	HM572544
L. decastes	Andersson 19901016/Swe/L	*Fagus* forest in deep tilth	HM572546
L. decastes	Bengtsson 19910929/Swe/L	Grass in hardwood forest	HM572545
L. decastes[a]	LAS 06-152/Swe/GB	Alongside compost heap	HM572547
L. decastes	Aase 19821031/Nor/O	Pasture	HM572543
L. decastes	Sundberg 20091007a/Jpn/GB	Grass lawn under *Pinus*	HM572548
L. decastes	Sundberg 20091007b/Jpn/GB	Grass lawn under *Pinus*	HM572549
L. fumosum	SJ 02-006/Swe/GB	Old moist *Picea* forest	HM572539
L. fumosum	Lipovac 20090903/Swe/GB	Mixed *Picea* forest	HM572538
L. fumosum	Sundberg 20090813/Swe/GB	*Pinus* moorland, sand	HM572537
L. cfr fumosum	LAS 00-144/Swe/GB	In hardwood forest	HM572541
L. cfr fumosum[a]	SJ 93-011/Swe/GB	Under hardwood	HM572542
L. cfr fumosum	Aase 19810721/Nor/O	Park in grass	HM572540
Lyophyllum sp.	Aase 19811014/Nor/O	In grass on open field	HM572550
Lyophyllum sp.	Cultivar/Jpn/GB	Unknown	HM572551
L. semitale	EL 187-09/Swe/GB	In grass, *Pinus*/*Betula*	HM572552

Jpn Japan, *Swe* Sweden, *Fin* Finland, *Nor* Norway

[a] The two specimens determined by morphology to be *L. loricatum* discussed in the text

Sivertsen, *L. sykosporum* Hongo & Clémençon, *Tephrocybe atrata* (Fr.) Donk, and *T. boudieri* (Kühner & Romagn.) Derbsch were included, and a sequence of *Lepista nebularis* (Fr.) Harmaja was selected as out-group.

Molecular methods and analyses

Sequences of the complete ITS region and 900 base pairs of the 5′ end of the nuclear LSU ribosomal DNA were generated. DNA extractions, polymerase chain reaction (PCR) reactions, and sequencing were performed as described in Larsson and Örstadius (2008). Sequences were edited and assembled using Sequencher 3.1 (Gene Codes, Ann Arbor, MI, USA). Sequences were aligned automatically using the MAFFT software (Katoh et al. 2005) and adjusted manually using the data editor in PAUP* (Swofford 2003). Sequence data were deposited in GenBank (Table 1) and alignment in TreeBASE (10823). Heuristic searches for the most parsimonious trees were performed using PAUP*. All transformations were considered unordered and equally weighted. Variable regions with ambiguous alignment were excluded and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed, saving 25 trees in each replicate. The relative robustness of clades was assessed by the bootstrap method, using 1000 heuristic search replicates with 100 random taxon addition sequence replicates and TBR swapping, saving 100 trees in each replicate.

Results

The aligned dataset comprised 47 taxa and had 1758 characters. After the exclusion of ambiguous regions, 1573 characters remained for the analysis. Of these, 1273 were constant, 138 were variable and parsimony uninformative, and 162 were parsimony informative. The maximum parsimony analysis yielded 24,725 equally most parsimonious trees (length 463, CI 0.7387, RI 0.8762), one of which is presented in Fig. 1. Bootstrap (BS) values above 50% are indicated above branches in the Fig. 1.

The bootstrap analysis recovered four major clades with support within *Lyophyllum* section *Difformia* corresponding to the species or species groups, *L. shimeji* (95%), *L. fumosum* (59%), *L. decastes* (100%), and *Lyophyllum* sp. (100%). All major clades include sequences from specimens originating from both Japanese and Fennoscandian specimens. Within the *L. shimeji* clade sequences of the Japanese specimens, the commercially sold cultivar and downloaded sequences of *L. shimeji* cluster with sequences of specimens originally identified as *L. decastes* and originating from lichen *Pinus* forest in different parts of northern Fennoscandia.

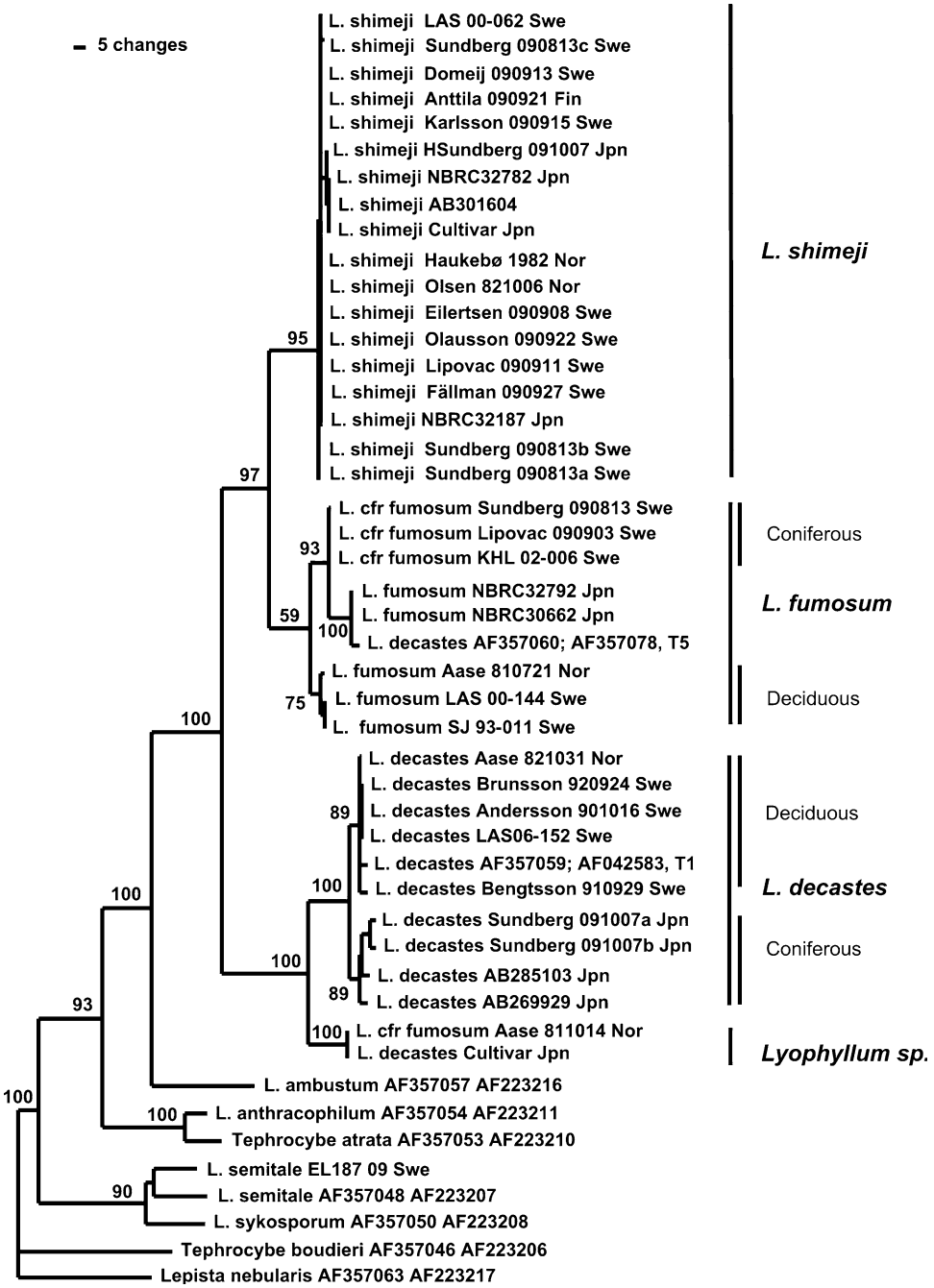

Fig. 1 One of the equally most parsimonious trees obtained from the maximum parsimony analysis, presented as a phylogram. Bootstrap values are indicated on *branches*. The four recovered major clades in the *L. decastes* complex have been *marked* and *named*. The ecology of subclades discussed in the text is indicated. The sequences marked T1 and T5 refer to Hofstetter et al. 2002. The two GenBank numbers (AF357060, AF357078) after *L. decastes* refer to the internal transcribed spacer (ITS) and large sub-unit (LSU) regions, respectively

The *L. fumosum* clade is further split into two subclades, one with specimens collected in deciduous forests in Norway and Sweden (75% BS) and one with three specimens collected in coniferous forests in Sweden, together with three downloaded sequences originating from Japan but with unknown ecology (93% BS). The Japanese sequences form a secondary subclade with 100% bootstrap support.

The *L. decastes* clade is also split into two subclades, one with specimens collected in deciduous forest in Norway and Sweden (89% BS) and one with sequences of two specimens collected in pine forests in Japan and two downloaded sequences originating from Japan but with unknown ecology (89% BS).

The *Lyophyllum* sp. clade includes the sequences of one specimen from Norway collected in grass on ruderal ground and the commercially sold *L. decastes* cultivar. The sequences of the two specimens identified as *L. loricatum* cluster in the *L. decastes* deciduous forest subclade and the *L. fumosum* deciduous forest subclade, respectively, indicating that they were misidentified.

Discussion

The results in this study show that the sequences of specimens from Fennoscandia identified as *L. decastes* form two clades corresponding to specific habitats. Specimens from sandy lichen pine forest in the northern regions cluster, strongly supported (95% BS), with specimens of *L. shimeji* from Japan, and must be considered as belonging to the same species (Fig. 1). The knowledge of the occurrence and distribution of *L. shimeji* (Fig. 2) in Fennoscandia is still insufficient. So far it is only known from oligotrophic forests dominated by Scots pine (*Pinus sylvestris*) and with a ground cover mainly consisting of a mosaic of lichens (*Cladonia* sp.), *Vaccinium vitis-idaea*, and *Calluna vulgaris*. In Japan, *L. shimeji* grows in mixed forests with *Pinus densiflora* and *Quercus serrata*. We believe that it is likely that the distribution of *L. shimeji* is wider than previously thought and that it may occur in the whole taiga region from Scandinavia to China and Japan.

Fig. 2 Photo of *Lyophyllum shimeji* from a lichen pine forest outside Hede, Härjedalen in Sweden

Sequences of specimens of *L. decastes* collected in deciduous forests in Sweden and Norway and the sequence of *L. decastes* named T1 in Hofstetter et al. (2002) form a strongly supported clade (100% BS) with sequences of *L. decastes* from Japan. Moncalvo and Clémençon (1994) showed that the *L. decastes* complex in Europe and Japan consists of five separate species denoted T1–T5 and that T1 was the only one encountered in both regions. Here we can confirm that sequences of European *L. decastes* and the Japanese hatake shimeji form a strongly supported clade. However, the clade is further subdivided and the sequences from Sweden and Norway, together with *L. decastes* T1, form one clade and the Japanese collections another (Fig. 1). The two Japanese specimens included in the present study were collected in pine forest. The sequence difference among the subclades may be due to the geographic distance or perhaps a difference in ecology, but further studies will have to evaluate the genetic variation observed.

Fries (1818) first described *L. decastes* as a species growing under *Quercus*, but later (Fries 1874) he emended the description to include also *Fagus*. This suggests that the clade identified here as *L. decastes*, with sequences of specimens originating from deciduous woods, represents *L. decastes* sensu stricto.

The clade named *Lyophyllum* sp. is apparently also a species that is closely related to *L. decastes* (Fig. 1). The two sequences originate from a specimen from Norway and a cultivar from Japan. Because we lack more specimens of this species we cannot give further comments on it.

The sequences of *L. fumosum* form a clade with rather low support (59% BS). This clade splits into two strongly supported subclades (Fig. 1) where the sequences of specimens from Sweden and Norway collected in deciduous forest are separated from those collected in coniferous forest (Fig. 1). This suggests that there are at least two species hidden under the name *L. fumosum* and that ecology is an important trait to take into account when delimiting the two.

Within the *L. fumosum* coniferous subclade (93% BS) the two sequences of *L. fumosum* originating from Japan, and the sequence named *L. decastes* T5 in Hofstetter et al. (2002), form a separate clade with strong support (100%). The sequence difference may again be interpreted as being due to the geographic distance. Moncalvo and Clémençon (1994) reported this taxon, shaka shimeji, as occurring in Japan and not yet found in Europe. We can now show that *L. fumosum* grows in coniferous forests in northern Fennoscandia.

L. fumosum was originally described by Persoon (1801) as a species occurring in forests with grass. Fries (1821) interpreted the species as growing in *Pinus* and *Betula* forests on gravelly ground, and later (Fries 1838) interpreted it as a species common in pine forest in mountainous areas. Even later, Fries (1874) changed his opinion about the habitat and interpreted it as a species occurring in deciduous forest, and in addition noted it to have a bitter taste. The variable descriptions therefore give few indications of which clade in our analysis could be suggested to represent *L. fumosum* sensu stricto. A stricter definition of *L. fumosum* should be based on sequenced specimens from the region in Europe where Persoon found his original material.

The two specimens in our study identified as *L. loricatum* based on morphology are most likely misidentified. The species seems to be rare and not so well known. In the current literature from the Nordic countries it is reduced to a variety of *L. decastes* and is said to differ from *L. fumosum* by having a burning aftertaste and a very thick cap cuticle (Vesterholt and Ludvig 2008). It was described by Fries (1838) as rare and growing in shady places under *Corylus* and later (Fries 1874) as growing in deciduous woods. Within the phylogenetic context developed here its identity remains unclear and further sequences from specimens fitting Fries' description are needed to resolve its taxonomic status.

In this study we show that *L. shimeji* is a species with a wider distribution than previously known and that it occurs in northern Fennoscandia, probably confined to Scots pine forests on lichen-clad sandy soil. Further, we have shown that *L. fumosum* is a heterogenous taxon with one form occurring in coniferous forests and another in deciduous forests. The result suggests that ecology is an important character when discriminating species in *Lyophyllum* section *Difformia*.

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